

Wood anatomy of *Zygodynum* (*Winteraceæ*); field observations

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Summary : Wood of eight populations of four species of *Zygodynum* is examined for the first time with cited herbarium specimens and with ecological observation. Distribution of anatomical characters within the genus shows specific and infraspecific distinctions. Some species have scalariform pitting on tracheids ; in other species such pitting is absent. A new subspecies is described, and the mechanism of opening of flowers in *Zygodynum* is explained.

Résumé : Le bois de huit populations appartenant à quatre espèces de *Zygodynum* est examiné pour la première fois d'après des échantillons d'herbier cités et en tenant compte d'observations écologiques. Des distinctions spécifiques et infraspécifiques sont faites en se basant sur des caractères anatomiques. Quelques espèces ont des ponctuations scalariformes sur les trachéides alors que de telles ponctuations manquent chez d'autres espèces. Une sous-espèce nouvelle est décrite et le mode d'ouverture des fleurs de *Zygodynum* est expliqué.

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INTRODUCTION

Wood anatomy of *Zygodynum*, a Winteraceous genus of six species endemic to New Caledonia (VINK, 1977) has not been studied except in brief and general ways. McLAUGHLIN (1933) describes wood of the genus without mentioning what species he had at hand. GUPTA (1934) studied samples claimed to be *Z. pomiferum* Baill. and *Z. vieillardii* Baill. BAILEY (1944a) studied a *Z. vieillardii* sample. The sources for the GUPTA and BAILEY studies were wood samples which came, via the Record Collection at Yale University, from the Commercial Museum of Philadelphia. No voucher specimens for these are known to exist. In view of the numerous misidentifications of *Zygodynum* species in the past (see VINK, 1977), the identity of the *Z. pomiferum* and *Z. vieillardii* wood samples is open to question.

Thus, there is no prior account of *Zygodynum* wood species-by-species. The present account is based on collections made on New Caledonia during 1977 and 1978 by the author ; one wood collection (*Z. pomiferum* subsp. *pomiferum*) was provided by Dr. Rudolf SCHMID of the University of California, Berkeley, who collected a specimen in 1978 during my

visit. Voucher specimens for these collections were determined with the aid of VINK's (1977) excellent monograph. VINK has also provided determinations on these specimens. The ecological regimes of the locations from which each of the collections came was observed, so that species distinctions in wood anatomy could be correlated with ecological features, as in my previous papers. The distinctions among the species and populations of *Zyggynum* are greater than one would have expected. However, the limited number of collections involved does not permit more than tentative conclusions on systematic distribution of anatomical characters within the genus.

Wood of *Zyggynum* is interesting in view of the fact that overlapping end walls of tracheids have been reported to bear scalariform pitting (BAILEY, 1944a; CARLQUIST, 1975), whereas the lateral walls always have circular pits. What is the significance of this conformation? Is it widespread or localized within the genus, and are there any ecological correlations of this feature?

MATERIALS AND METHODS

Wood samples and herbarium specimens were prepared from materials collected in the field. Bark was removed from woods. In humid air, woods do not dry readily without molding, and in brief visits to New Caledonia, woods could not be air-dried in the time available. Consequently, wood samples were covered with paraformaldehyde, enclosed in plastic bags, shipped, and dried after arrival in California, as described earlier (CARLQUIST, 1980). In order to prepare sections and macerations, wood samples were boiled in water. Samples too hard to be sectioned readily were treated with the ethylene diamine method (КУРАЧКА, 1977). Sections and macerations were stained with safranin. Some roots as well as stems were studied. The illustrations show stem wood unless legends indicate otherwise. Herbarium vouchers are located in RSA.

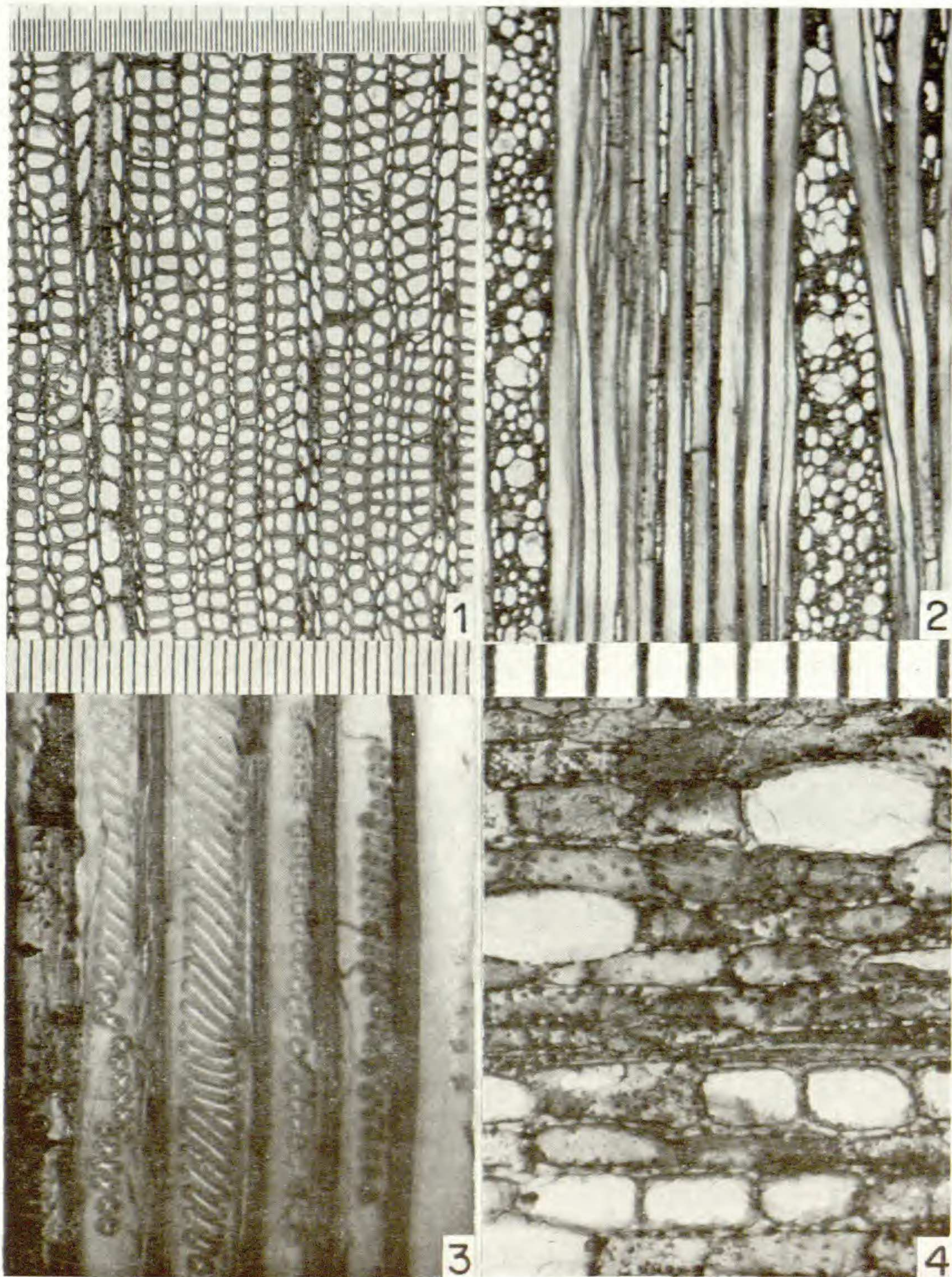
ANATOMICAL OBSERVATIONS

TRACHEIDS

Tracheid lengths vary within *Zyggynum*. Because tracheid lengths in vesselless angiosperms have been found to be correlated roughly with plant size (CARLQUIST, 1975), the diameter of the wood sample is placed in parentheses in the following list of mean tracheid lengths.

Tracheid lengths in stems : *Z. baillonii* Tieghem, *Carlquist 15605* (5.2 cm), 5063 μm ; *Z. baillonii*, *Carlquist 15609* (4.0 cm), 4809 μm ; *Z. bicolor* Tieghem, *Carlquist 744* (7.0 cm), 4400 μm ; *Z. bicolor*, *Carlquist 15591* (15.0 cm), 4766 μm ; *Z. mackeei* Vink subsp. *paniense* Carlquist, *Carlquist 15580* (2.7 cm), 3636 μm ; *Z. pomiferum* Baill. subsp. *balansæ* (Tieghem) Vink, *Carlquist 15595* (4.5 cm), 3252 μm ; *Z. pomiferum* subsp. *balansæ*, *Carlquist 15612* (3.5 cm), 2157 μm ; *Z. pomiferum* subsp. *pomiferum*, *Schmid 1978-179* (3.0 cm), 3790 μm .

Tracheid lengths in roots : *Z. baillonii*, *Carlquist 15609*, 4139 μm ; *Z. pomiferum* subsp. *balansæ*, *Carlquist 15595*, 3025 μm .



Pl. 1. — *Zygogynum bicolor* Tieghem, *Carlquist 744*, wood sections : 1, transection, showing thin-walled tracheids and bands of axial parenchyma ; 2, tangential section ; etheral oil cells visible in the multiseriate rays ; 3, radial section, showing scalariform pitting on tracheid overlap areas ; 4, radial section, showing ray cells ; markedly procumbent ray cells in center. Magnification scale for 1, 2, above 1 (finest divisions = 10 μ m). Scale for 3 above 3 (divisions = 10 μ m). Scale for 4 above 4 (divisions = 10 μ m).

There is some correlation between stem diameter and tracheid length, although obviously a poor one. *Zygogynum bicolor* has tracheids shorter than one might expect on the basis of the sizes of stems studied; or, alternatively, *Z. baillonii* could be said to have tracheids longer than one might expect. The collection 15612 of *Z. pomiferum* subsp. *balansæ* has notably short tracheids. These taxa are also of interest with respect to end walls on tracheids, as noted below.

Tracheid wall thicknesses vary in *Zygogynum*. Thin-walled tracheids were observed in *Z. bicolor* (Pl. 1, 1), both collections. Especially thin-walled tracheids occurred in non-annual bands in *Z. mackeei* subsp. *paniense* (Pl. 2, 1) and the collection 15612 of *Z. pomiferum* subsp. *balansæ* (Pl. 3, 1). These may have been produced in response to seasonal events, but radial tracheid diameters give no hint of seasonality in woods of *Zygogynum*. Other than the presence of an occasional zone of thin-walled tracheids, one can cite no growth rings in *Zygogynum*.

Pitting on secondary xylem tracheids of *Winteraceæ* is well known to consist basically of bordered circular pits, somewhat more dense on overlapping end walls than on lateral radially-oriented walls, and relatively sparse but definitely present on tangentially-oriented walls (BAILEY, 1944a). However, the overlapping radially-oriented end walls of tracheids bear scalariform pitting in *Bubbia* and *Zygogynum* (BAILEY, 1944a; CARLQUIST, 1975). The collections of *Zygogynum* studied here differ in degree of presence of this scalariform pitting:

Scalariform pitting not observed on tracheids:

- Z. baillonii*, Carlquist 15609 (root and stem);
- Z. bicolor*, Carlquist 15591;
- Z. pomiferum* subsp. *balansæ*, Carlquist 15595 (root and stem);
- Z. pomiferum* subsp. *pomiferum*, Schmid 1978-179.

Scalariform pitting on some tracheids:

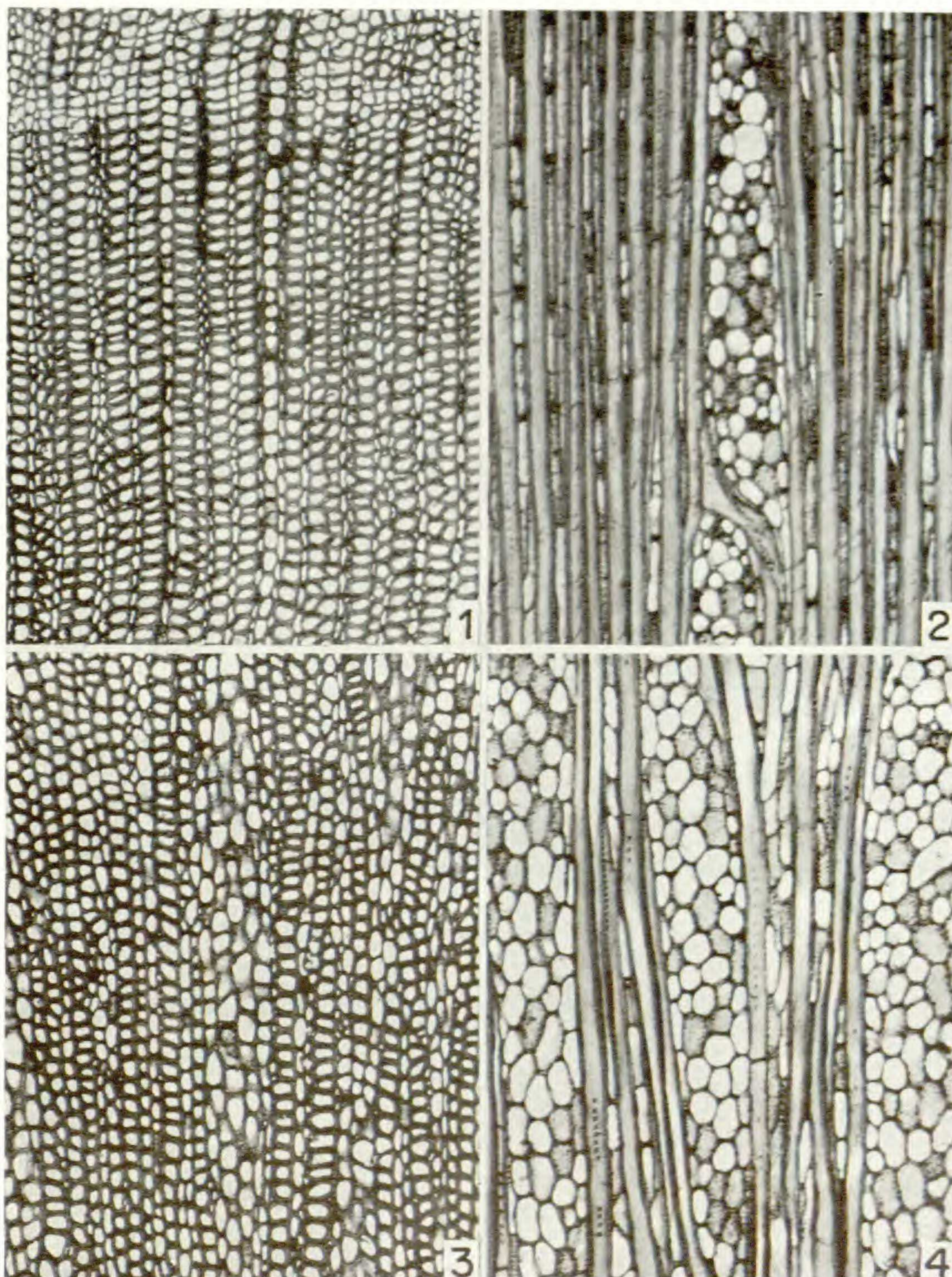
- Z. baillonii*, Carlquist 15605;
- Z. bicolor*, Carlquist 744 (Pl. 1, 3; Pl. 4, 1, 2);
- Z. mackeei* subsp. *paniense*, Carlquist 15580 (Pl. 4, 3).

Scalariform pitting abundant on end walls of nearly all tracheids:

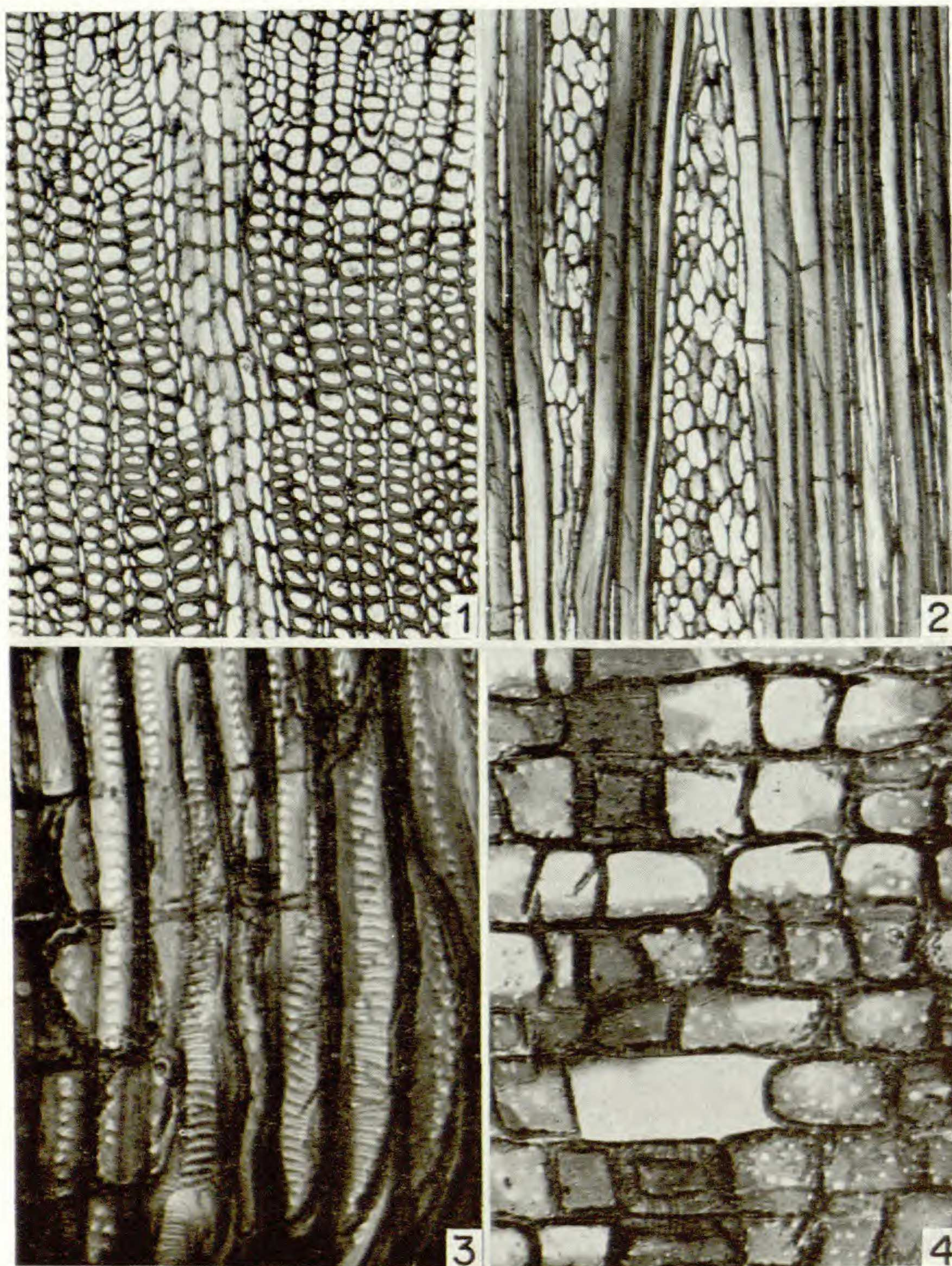
- Z. pomiferum* subsp. *balansæ*, Carlquist 15612 (Pl. 3, 3; Pl. 4, 4).

Not shown here, except in Pl. 3, 3, are crowded circular bordered pits on end walls of tracheids. *Zygogynum bicolor* (Carlquist 15591) showed such crowded pits on end walls; the pit apertures of these pits are wider, more gaping, than those of lateral wall pits. This might compensate for lack of scalariform pitting in this collection, since the pit area interconnecting tracheids in a vertical file might be close to that on scalariformly pitted end walls.

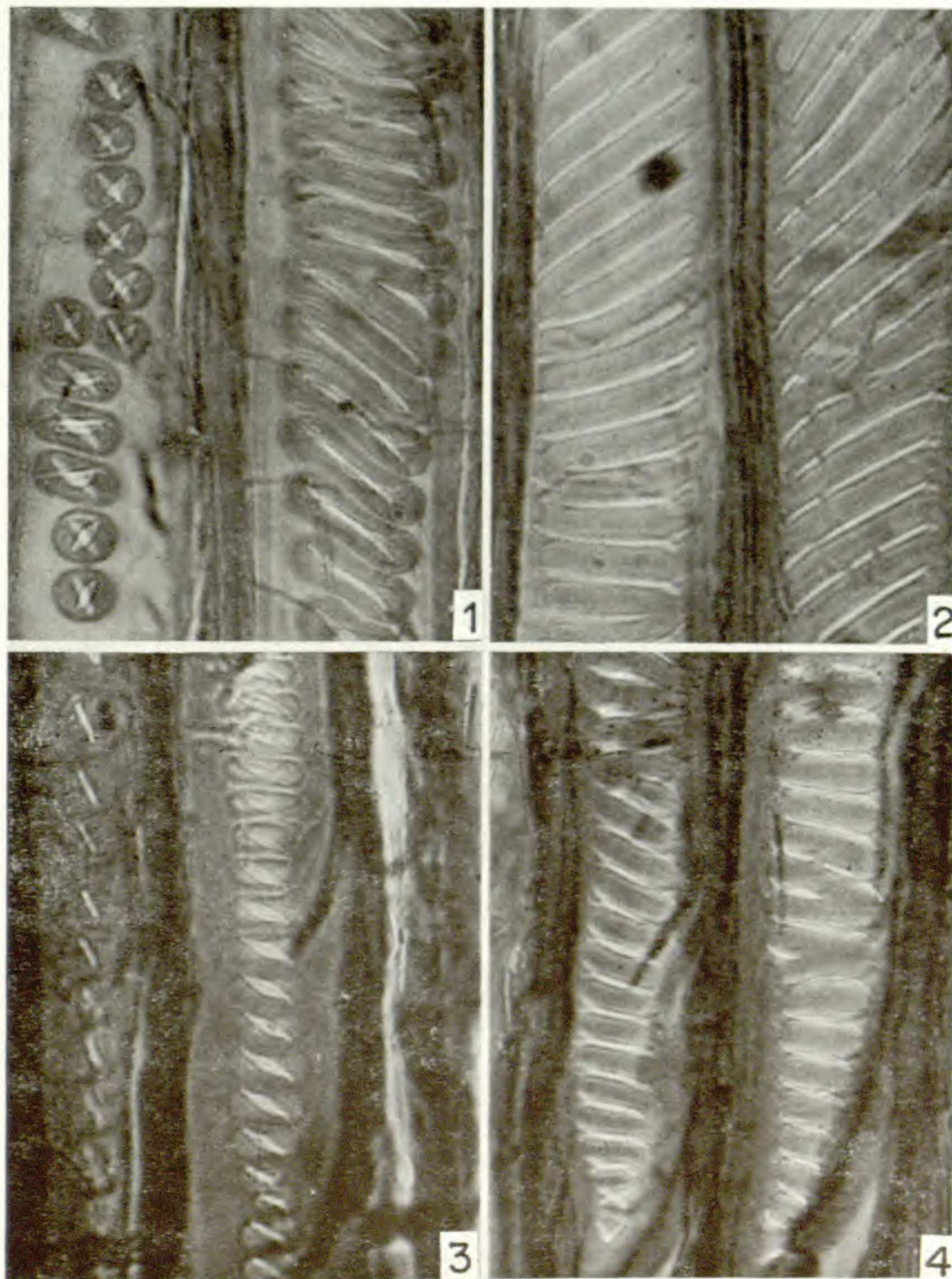
The significance of scalariform pitting on end walls does appear to be a maximizing of conductive area, as suggested earlier (CARLQUIST, 1975). It can also be regarded as a relictual feature, provided that "relictual" is understood in a special sense. *Winteraceæ* have the genetic information to manufacture scalariform pits on both lateral and end walls of tracheids, as shown by the fact that metaxylem tracheids in *Zygogynum*, as well as in other genera, bear such pitting. BAILEY (1944b) has suggested that pitting of primary



Pl. 2. — *Zygodinium* wood sections : *Z. mackeei* Vink subsp. *paniense* Carlquist, *Carlquist 15580* : 1, transection ; 2, tangential section ; uniseriate rays mostly composed of erect cells. — *Z. pomiferum* Baill. subsp. *balansæ* (Tieghem) Vink, *Carlquist 15595*, wood from root : 3, transection ; large multiseriate ray in center ; 4, tangential section, showing abundant ray tissue. Magnification scale for 1-4, above Pl. 1, 1.



Pl. 3. — *Zyggynum pomiferum* Baill. subsp. *balansæ* (Tieghem) Vink, *Carlquist 15612* : 1, transection ; 2, tangential section, strands of axial parenchyma visible to right of the ray ; 3, radial section, showing at right scalariform pitting on overlap areas of tracheids ; 4, radial section of ray showing thin-walled cells, sclereids, and (space below) remnant of an ethereal oil cell. Magnification scale for 1 & 2 above Pl. 1, 1. Scale for 3 above Pl. 1, 3. Scale for 4 above Pl. 1, 4.



Pl. 4. — *Zygogynum*, radial sections of wood to show scalariform pitting on overlap areas of tracheids : *Z. bicolor* Tieghem, *Carlquist 744* : 1, scalariform pitting plus circular pits ; 2, scalariform pitting, a few pits subdivided. — *Z. mackeei* Vink subsp. *paniense*, *Carlquist 15580* : 3, scalariform and circular pits. — *Z. pomiferum* Baill. subsp. *balansæ* (Tieghem) Vink, *Carlquist 15612* : 4, scalariform pitting. Magnification scale for all above Pl. 1, 4.

xylem is more conservative in evolution than that of secondary xylem, and the primary xylem is a kind of "refuge". In this case, one would say scalariform end walls on secondary xylem tracheids represents a continuation of the primitive pattern, a continuation adaptive because conduction is maximized; lateral walls of secondary xylem tracheids then represent a condition maximal for strength, since scalariform pitting on lateral walls is weaker than scattered circular bordered pits. A pattern of scalariform pitting on both end walls and lateral walls would result in excessively weak tracheids in a wood like that of *Zygogynum*, in which no alternation between wide and narrow tracheids with season, as in *Trochodendron*, is present (CARLQUIST, 1975).

One can envision that increase in conductive ability provided by scalariform pitting on the end walls does not seriously lessen the mechanical strength. What is evident from the present study is that presence of scalariform pitting on the end walls of the secondary xylem tracheids is at least somewhat related to habitat. The collection of *Z. bicolor* which has the scalariform pitting is in a much more exposed locality (stunted forest at the periphery of the summit plateau, Plateau de Dogny) than the collection which lacks such pitting (understory of tall wet forest, mid-elevations of Mt. Panié). Scalariform pitting on end walls is only truly abundant in the collection 15612 of *Z. pomiferum* subsp. *balansæ*. This distinctive plant is from a curious kind of locality for the genus: understory, banks of a seasonal stream, Pic du Pin, Plaine des Lacs, ca. 150 m elevation. This site may well feature higher transpiration at such a low, warm, elevation; therefore, a higher conductive capacity as provided by the scalariform end walls would be comprehensible.

The collections which have scalariform pitting on some tracheids also tend to have shorter tracheids than one would expect, based upon the diameter of the wood sample from which they come. In vessel elements, shortness is related to drier habitats (CARLQUIST, 1975); perhaps in tracheids with scalariform end walls some such correlation also obtains, but the present material is by no means conclusive.

AXIAL PARENCHYMA

The species are distinctive in modes of axial parenchyma they exhibit. They can be grouped as follows:

Parenchyma diffuse, scarce:

Z. pomiferum subsp. *pomiferum*, Schmid 1978-179.

Parenchyma diffuse, not rare:

Z. baillonii (15605; 15609 root and stem);

Z. pomiferum subsp. *balansæ* (15595: Pl. 2, 3).

Parenchyma diffuse to diffuse-in-aggregates (tangential pairs of cells):

Z. mackeei subsp. *paniense* (15580: Pl. 2, 1).

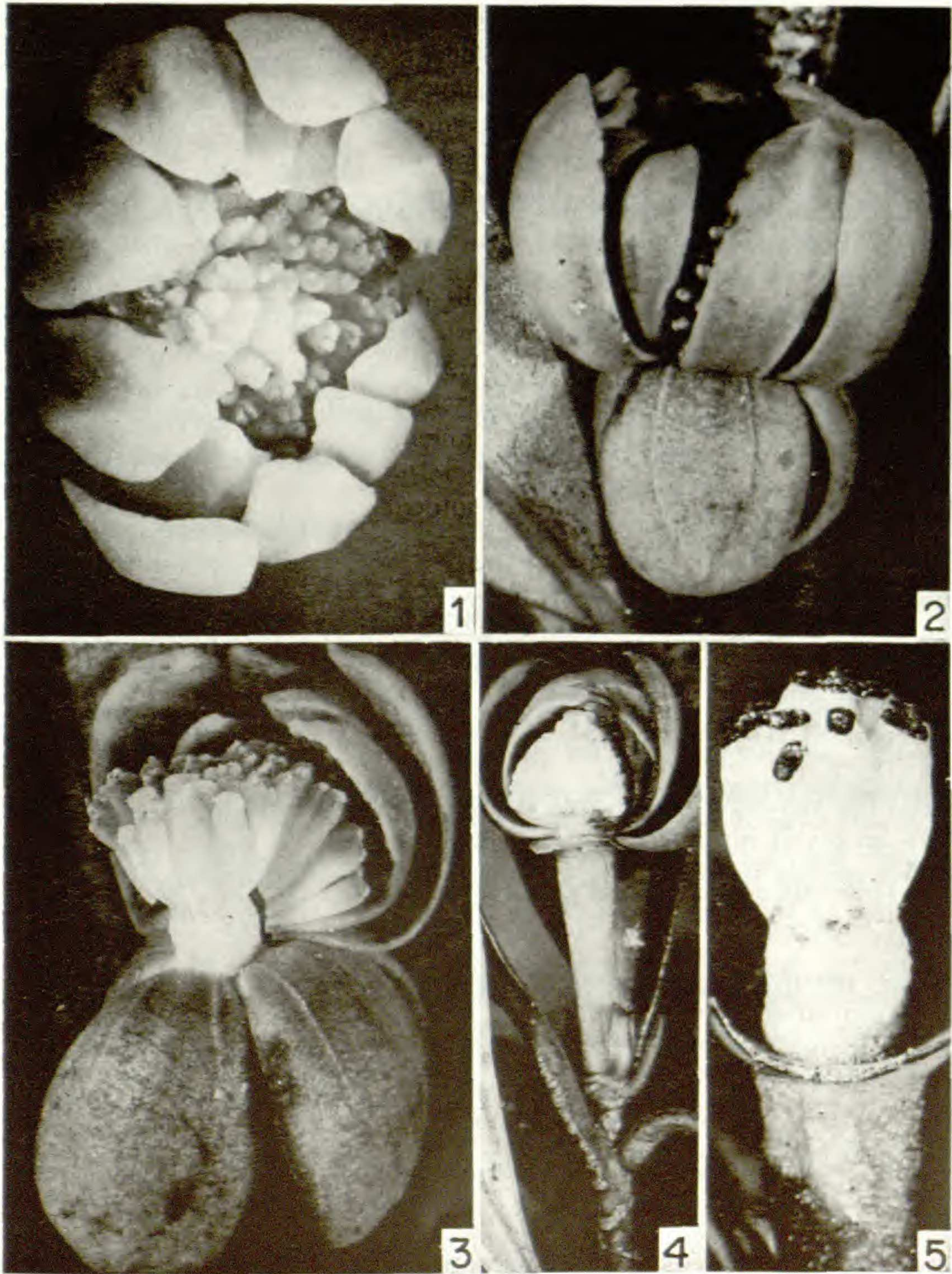
Parenchyma diffuse-in-aggregates, forming bands one cell thick:

Z. bicolor (744: Pl. 1, 1);

Z. pomiferum subsp. *balansæ* (15162: Pl. 3, 1, 2).

Parenchyma narrow banded, bands two to three cells thick:

Z. bicolor (15591).



Pl. 5. — *Zygogynum mackeei* Vink subsp. *paniense* Carlquist, *Carlquist 15580*, view of flower : 1, flower at anthesis, seen from above ; 11 carpels in center ; 2, flower at anthesis, seen from side ; four outer petals are recurved ; 3, inner petals fallen from flower, showing fully turgid stamens ; 4, flower and pedicel, petals dissected away, of a flower just before anthesis ; the stamens have not yet imbibed water and are not swollen ; 5, carpels after petals and stamens have fallen. The carpels in this specimen are about 7 mm long ; the flower in 1 would measure 15 × 18 mm.

Although BAILEY (1944a) reported part of this range for *Winteraceæ* as a whole, the above shows that particular types may characterize populations and species. I am unable to confirm McLAUGHLIN's (1933) report of terminal parenchyma in the genus.

RAY PARENCHYMA

The rays of *Zygogynum* correspond to KRIBS's description of Heterogeneous Type I: multiseriate rays have a body composed of procumbent cells; sheathing cells at the periphery and in the wings are most commonly erect, rarely procumbent; uniseriate rays are heterocellular, composed of erect and procumbent cells, but more commonly erect ones. As stems increase in diameter, erect ray cells become more common (Pl. 1, 2, 4). In stems of less than optimal diameter for the genus, procumbent cells are not so markedly procumbent in multiseriate rays (Pl. 2, 2, 4; Pl. 3, 2, 4). This corresponds to a pattern of subdivision of fusiform cambial initials, a pattern which often continues to occur over a period of years in many dicotyledons.

Ray cells in *Zygogynum* are basically moderately thick-walled, with the wall clearly lignified (Pl. 1, 4; Pl. 3, 4). However, ethereal oil cells may be found (Pl. 1, 4, bottom left and above, left and right; Pl. 3, 4, space near bottom). Ethereal oil cells were not observed in *Z. pomiferum* subsp. *balansæ* (15595) and *Z. pomiferum* subsp. *pomiferum* (Schmid, 1978-179), but they were observed in the remaining six collections studied here. In the distinctive collection 15612, currently termed a population of *Z. pomiferum* subsp. *balansæ*, ethereal oil cells are present, but in addition, sclerosed ray cells occur in multiseriate rays (Pl. 3, 4).

At least a few ray cells in each collection were observed to have bordered pits. These borders were observed in sectional view, not face view, in radial sections. One cannot see the borders readily in face view. Marked borders on both tangential and radial walls of ray cells, such as those GARRATT (1933) figured for *Cephalosphæra* of the *Myristicaceæ*, are not present.

Roots of *Z. pomiferum* subsp. *balansæ* (Pl. 2, 4) proved to have much more ray tissue, as seen in tangential section, than stems of that collection. A greater proportion of ray to axial tissue in roots as compared to stems is generally not uncommon in dicotyledons, although few studies offer observations or quantitative data on this point. Greater amounts of ray tissue in roots as compared to stems may relate to a lesser mechanical function of roots, but also possibly a greater storage function of roots as compared to stems.

FIELD OBSERVATIONS AND SYSTEMATIC CONSIDERATIONS

In collecting and identifying *Zygogynum* in New Caledonia, I found VINK's (1977) monograph to be quite accurate. VINK has identified species quite accurately. As he notes, most of the species are variable. One can say that geographically quite distinct populations of a given species in this genus are often different to an appreciable degree in morphological features. The variability of species in what many would regard as an ancient group is a curious phenomenon. On account of the distinctive populations within

Zygogynum, one could easily describe infraspecific taxa, but that would be premature in many cases. Most species are known only from a few collections, making assessment of infraspecific taxa difficult at present. However, in 1978 I collected at 1450 m on Mt. Panié a shrubby (2-3 m) *Zygogynum* referable to *Z. mackeei*, but clearly a high-altitude variant (Pl. 5). Comparison to VINK's description of the species reveals a number of differences in this variant. In the following description, VINK's characters for typical *Z. mackeei* are given in parentheses. The high elevation variant has only one flower per inflorescence (3-5); the pedicel is two-angled (2-4), 10×2 mm ($15-28 \times 2-4$ mm). The carpels are 9-11 in number (14-19). The leaf blades are $5-7.5 \times 2-3$ cm ($10.5-22 \times 3.5-7$ cm). The petioles and midrib are rounded in sectional view (angular in typical *Z. mackeei*), both in fresh and in dried material. On the basis of these distinctions, a new subspecies is proposed :

***Zygogynum mackeei* Vink subsp. *paniense* Carlquist, subsp. nov.**

Ab specie typica foliorum lamina $5-7.5 \times 2-3$ cm, petiolo 7-8 mm longo, pedicello 10×2 mm, stigmatibus 9-11, differt.

TYPE : *Carlquist 15580*, 18.8.1978 (holo-, RSA ; iso, P, L).

The distinctive population of *Z. pomiferum* subsp. *balansæ* (*Carlquist 15612*) from Pic du Pin (terminus of the range of this species) might eventually deserve taxonomic recognition. As noted above, it is distinctive in its relatively short tracheids which commonly bear scalariform pitting on the long end walls ; the rays have ethereal oil cells and sclerosed cells ; axial parenchyma is present as diffuse-in-aggregates. These features differ from those of the other *Z. pomiferum* subsp. *balansæ* population examined.

Field observations on flowers of *Z. mackeei* subsp. *paniense* showed clearly distinctive features of opening of *Zygogynum* flowers. These features, in fact, also occur in flowers of *Drimys*, *Exospermum*, and *Pseudowintera*, in my experience. The filaments of *Z. mackeei* subsp. *paniense* swell, in mature flowers, sometimes during a rainy period. The marked swelling — most noticeable at the distal end of the stamens — forces flowers open (compare Pl. 5, 1 & 3, with Pl. 5, 4). This is interesting, because drying mechanisms (xerochasy) rather than water imbibition mechanisms (hygrochasy) are thought by some responsible for opening of flowers in many angiosperms. THIEN (1980) shows that *Zygogynum* is protogynous ; I can confirm this. One can easily note non-receptive stigmas because the accumulate tannins so conspicuously. All genera of *Winteraceæ* (except *Tasmannia*, which is dioecious) are protogynous, in my experience, and the vast majority of *Magnoliales* (*Annonales*) evidently are also.

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